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Asymmetric development of dorsal and ventral attention networks in the human brain



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ABSTRACT

Two neural systems for goal-directed and stimulus-driven attention have been described in the adult human brain; the dorsal attention network (DAN) centered in the frontal eye fields (FEF) and intraparietal sulcus (IPS), and the ventral attention network (VAN) anchored in the temporoparietal junction (TPJ) and ventral frontal cortex (VFC). Little is known regarding the processes governing typical development of these attention networks in the brain. Here we use resting state functional MRI data collected from thirty 7 to 12 year-old children and thirty 18 to 31 year-old adults to examine two key regions of interest from the dorsal and ventral attention networks. We found that for the DAN nodes (IPS and FEF), children showed greater functional connectivity with regions within the network compared with adults, whereas adults showed greater functional connectivity between the FEF and extra-network regions including the posterior cingulate cortex. For the VAN nodes (TPJ and VFC), adults showed greater functional connectivity with regions within the network compared with children. Children showed greater functional connectivity between VFC and nodes of the saliency network. This asymmetric pattern of development of attention networks may be a neural signature of the shift from over-representation of bottom-up attention mechanisms to greater top-down attentional capacities with development.

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1. Introduction

It is well established that there are two partially segregated attention networks in the human brain; the so-called dorsal and ventral attention networks (Corbetta and Shulman, 2002). The dorsal attention network (DAN) includes bilateral intraparietal sulcus (IPS) and the frontal eye fields (FEF), and is concerned with orientating ones focus on a particular task. Previous work has demonstrated that the FEF and IPS exert top-down influences on visual areas during visual orienting of attention (Bressler et al.,

2008). The DAN shows sustained activation when focusing attention on an object (Corbetta et al., 2008), and is thought to be responsible for goal-directed, top-down processing (Corbetta and Shulman, 2002). The second network, the ventral attention network (VAN), is comprised of the temporoparietal junction (TPJ) and ventral frontal cortex (VFC), and responds to relevant external environmental stimuli. The VAN is dominant in the right hemisphere, and is generally activated when an unexpected event occurs and breaks ones attention from the current task (i.e. bottom-up processing) (for a full review of the DAN & VAN see Corbetta et al., 2008). This network's key function is to direct attention to stimuli outside of the current focus of processing and is referred to as the 'circuit breaking' section of the two attention networks (Shulman et al., 2002). Corbetta and colleagues argue that only behaviorally relevant

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environmental stimuli trigger the VAN, and that the response of the VAN is suppressed when irrelevant information is presented (Corbetta et al., 2008). The VFC has been identified to be mainly active when reorienting is unexpected and requires cognitive control or is coupled to a response (Corbetta and Shulman, 2002). The two core regions of the VAN are typically co-activated, as well as functionally connected (Fox et al., 2006; He et al., 2007).

Another brain system termed the 'salience network' has also been linked with functions that partially overlap with functions ascribed to the VAN, including responding to behaviorally relevant stimuli (Seeley et al., 2007). The salience network is comprised of dorsal anterior cingulate, subcortical, and limbic structures, as well as bilateral anterior insular cortices adjacent to or overlapping the VFC node of the VAN (Uddin, 2015), and has been demonstrated to show within- and between-network developmental changes including increases in functional and structural connectivity with age (Uddin et al., 2011). While some investigators see the high degree of functional and anatomical overlap between the VAN and salience network as evidence that they are part of the same system (Kucyi et al., 2012), the majority have conceptualized these networks as distinct entities (Cole et al., 2013; Power et al., 2011).

Resting state fMRI (R-fMRI) studies capitalize on the fact that large-scale neurocognitive networks can be reliably identified in the absence of task-related processing (Biswal et al., 1995; Damoiseaux et al., 2006; Smith et al., 2009). Fox et al. (2006) were the first to use R-fMRI to examine attention networks in the human brain. They identified a bilateral DAN and right lateralized VAN solely on the basis of seed-based functional connectivity analyses of resting state fMRI data, thus providing evidence that these attention networks are intrinsically coupled in the brain.

The use of R-fMRI to address developmental questions allows us to avoid many of the issues related to task performance that can confound interpretation of developmental neuroimaging findings (Casey et al., 2005; Uddin et al., 2010). R-fMRI studies have demonstrated that over the lifespan, the long-range connections within the DAN become more dominant until around the age of ~30 years (Cao et al., 2014). Cao and colleagues found inverted U-shaped trajectories mainly within the DAN and language regions, which are argued to be amongst the last regions to mature (Casey et al., 2000). This research is in line with previous studies which suggest that short-distance functional connectivity is greater in children than it is in adults (Dosenbach et al., 2010; Fair et al., 2009; Supekar et al., 2009) and that the long-range connections observed in adults are enhanced throughout development (Fair et al., 2009; Kelly et al., 2009; Supekar et al., 2009). It is argued that the process of synaptic "pruning" in which the abundance of short-range connections in typically developing children are eliminated, generally in the pubertal stage of development, contributes to the prominence of long-range connectivity in adults (Huttenlocher, 1990).

Though there is an abundance of literature surrounding human attention networks, there is surprisingly little research that focuses on the typical development of these networks (Konrad et al., 2005). A previous independent component analysis (ICA) study examining developmental

differences in the dorsal attention network found stronger within-network connectivity in the DAN in 11–13 year-old children compared with 19–25 year old adults (Jolles et al., 2011). Seed-based approaches can offer complementary information to that derived from ICA, namely allowing for hypothesis-driven analyses of specific functional networks of interest (Uddin et al., 2010). To the best of our knowledge, no previous studies have used seed-based approaches to explore developmental differences in functional connectivity of DAN and VAN nodes, or inter-network relationships.

Here we use R-fMRI to explore the typical development of the DAN and VAN in the human brain. We aimed to test the following hypotheses: (1) R-fMRI can be used to identify the DAN and VAN in children, and these networks have a similar topological organization to that observed in adults; (2) long-range functional connectivity of DAN and VAN nodes will be more predominant in adults than in children; and (3) between- and within-network functional connectivity patterns will show developmental changes.

2. Materials and methods

2.1. Participants and data acquisition

The present study included a total of 60 healthy, right-handed neurotypical individuals from the publicly available Autism Brain Imaging Data Exchange (ABIDE; <http://fcon.1000.projects.nitrc.org/indi/abide/>) (Di Martino et al., 2014). We examined only data collected from the New York University Langone Medical Center (NYU) for consistency. All participants had a full-scale IQ score of >80, and the groups did not differ significantly on IQ. The group of 60 was split into two groups of children (mean age: 10.2, range 7–12, 11 females) and adults (mean age: 24.2, range 18–31, 6 females) consisting of 30 participants each (Table 1). Participants were also carefully selected based on motion parameters. No participant was selected with absolute displacement > 1.95 mm. The range of motion parameters for the child group was 0.09–1.95 mm mean absolute displacement (0.27 ± 0.33). The range of motion parameters for the adult group was 0.15–0.89 mm mean absolute displacement (0.30 ± 0.18). No group differences in absolute displacement were observed ($p=0.7$). The NYU institutional review board approved all procedures for data collection and sharing. Written informed consent was obtained from each participant.

Table 1
Participant characteristics.

Characteristic	Children ($n=30$) (standard deviation) [range]	Adults ($n=30$) (standard deviation) [range]
Age (years)	10.2 (1.74) [7.19–12.97]	24.2 (3.34) [18.59–31.78]
Sex (No.)		
Male	19	24
Female	11	6
Full-Scale IQ	116.17 (13.89) [80–142]	114.93 (10.09) [91–139]

Inclusion as a typically developing individual (TD) was based on the absence of any current Axis-I disorders as determined by the Kiddie-Schedule for Affective Disorders and Schizophrenia-Present and Lifetime Version (KSADS-PL) administered to each child and his/her parent, and the Structured Clinical Interview for DSM-IV Axis I Disorders-Non-patient Edition (SCID-I/NP) and Adult ADHD Clinical Diagnostic Scale (ACDS) interviews for adults.

All subjects were scanned using a 3T Allegra, in a separate visit following the diagnostic assessment (typically within 3 months). The R-fMRI scans were collected using an echo-planar imaging (EPI) sequence (TR = 2000 ms; TE = 15 ms; flip angle = 90°; FOV = 240 mm; voxel size = 3 mm × 3 mm × 4 mm; number of slices = 33, 4 mm slice thickness). The scan lasted for 6 min, which consisted of 180 volumes. Participants were asked to relax with their eyes open, while a white cross hair against a black background was projected on a screen.

A high-resolution T₁-weighted anatomical image was acquired using a magnetization prepared gradient echo sequence (TR = 2530 ms; TE = 3.25 ms; inversion time = 8.07 min; flip angle = 7°; 128 slices; 1 volume FOV = 256 mm). All details regarding scanning protocols are outlined in (Di Martino et al., 2014).

2.2. Region-of-interest (ROI) selection

Four ROIs were selected based on previous research conducted by Fox and colleagues (Fox et al., 2006). In this earlier study, four ROIs (two in the DAN and two in the VAN) were determined via meta-analyses. In the DAN, the ROIs were located in right intraparietal sulcus (IPS; 32, −56, 54) and frontal eye fields (FEF; 28, −8, 52), and in the VAN the ROIs were located in right temporoparietal junction (TPJ; 60, −48, 22) and ventral frontal cortex (VFC; 42, 20, −6). For the current study, spherical ROIs were created with a radius of 6 mm based on these coordinates as reported by Fox et al. (2006). Exploratory follow-up analyses related to the salience network were conducted using a seed in the anterior cingulate cortex (ACC; 6, 24, 32) derived from a previous study (Uddin et al., 2011). All coordinates are reported in MNI standard space.

2.3. Data preprocessing

Data were preprocessed using the Data Processing Assistant for Resting-state fMRI Advanced Edition (DPARSF-A) toolbox, which is part of the Data Processing and Analysis of Brain Imaging (DPABI) toolbox version 3.1, (<http://rfmri.org/dpabi>) (Chao-Gan and Yu-Feng, 2010). The first 5 volumes were removed from each subject's resting-state fMRI data. Data were preprocessed in series of steps including slice-timing correction, brain extraction of T1 images, and segmentation using SPM priors for cerebrospinal fluid (CSF) and white matter (WM). We used the WM and cerebral CSF mean time-series as nuisance regressors in the general linear model (GLM) to reduce the influence of physiological noise (Margulies et al., 2007). Global signal regression was not used (Saad et al., 2012). Additionally, we regressed out the nuisance covariates using the Friston 24-parameter model (Friston et al., 1996)

and applied a band pass filter capturing the fMRI signal between the frequencies 0.01–0.08 Hz. The data were spatially smoothed with a 5 mm full-width half-maximum Gaussian kernel. To further reduce motion-related artifacts we “scrubbed” our data using the cut (delete) option available in the DPABI-A toolbox using the following parameters: FD threshold for bad time points = 0.5, scrubbing time points before bad time points = 1, scrubbing time points after bad time points = 2 (Power et al., 2012). The data were registered to the subject's individual anatomical space and then into MNI standard space.

2.4. Individual and group-level analyses for seed-based whole-brain functional connectivity analyses

For each participant, we extracted the mean time-series of each of the four attention network ROIs individually using the functional connectivity voxel-wise option in the REST toolbox version 1.8 (http://www.restfmri.net/forum/REST_V1.8). We then compared whole-brain functional connectivity patterns between adults and children for each ROI. Data were corrected for multiple comparisons using Gaussian Random Field Theory Multiple Comparison Correction (voxel-level p -value = .01; cluster-level p -value = .05, two-tailed). Two-tailed t -tests between results for the children and adult groups were conducted for each ROI. These analyses produced thresholded Z-score maps for each of the four ROIs.

2.5. Seed-to-seed analyses within networks

In addition to the seed-based whole-brain functional connectivity analyses, which showed developmental differences in functional connectivity of specific DAN and VAN ROIs, we also conducted analyses between seed regions within the DAN and within the VAN. We used the same coordinates listed in Section 2.2 to represent the two seeds within each network. Using the REST toolbox we calculated pair-wise functional connectivity between the seeds within the DAN (rIPS-rFEF) and within the VAN (rVFC-rTPJ). Two-sample t -tests were conducted to explore group differences in within-network functional connectivity in the two attention networks.

2.6. Seed-to-seed analyses between networks

To explore potential group differences in between-network functional connectivity, we conducted the following seed-to-seed correlation analyses of the following ROI pairs: rIPS-rVFC, rFEF-rTPJ, rIPS-rTPJ, rFEF-rVFC. Two-sample t -tests were conducted to explore group differences in between-network functional connectivity.

3. Results

3.1. DAN and VAN topological organization in children and adults

To visualize the organization of the DAN and VAN in children and adults, the whole-brain functional connectivity maps associated with each region of interest within each

network are depicted in Fig. 1. As can be seen in Fig. 1A, the overlap of the functional connectivity map of the IPS seed (blue) and the FEF seed (purple) delineates the regions described in (Corbetta and Shulman, 2002) and (Fox et al., 2006) as belonging to the DAN. The areas of overlap (violet) include bilateral IPS, bilateral FEF, and ventral temporal visual areas, in both children and adults. As can be seen in Fig. 1B, the overlap of the functional connectivity maps of the TPJ (blue) and VFC (purple) delineates the regions previously described as belonging to the VAN. The areas of overlap (violet) include middle frontal gyrus, anterior insula, VFC and TPJ, in both children and adults.

3.2. Developmental differences in whole-brain functional connectivity of dorsal attention network nodes

For both adults and children, IPS showed strong functional connectivity with other regions of the DAN including frontal eye fields and visual cortical regions. For both adults and children, FEF showed strong functional connectivity with the entire DAN including intraparietal and visual cortical regions.

We found that for both ROIs representing the DAN (IPS and FEF), children showed greater functional connectivity within the network (e.g. with the IPS) than did adults. Adults showed greater functional connectivity of the FEF with regions outside of the DAN (e.g. posterior cingulate cortex, PCC) than did children (Fig. 2). Table 2 lists coordinates of significant group differences in functional connectivity for each ROI.

3.3. Developmental differences in whole-brain functional connectivity of ventral attention network nodes

For both adults and children, TPJ showed strong functional connectivity with other regions of the VAN

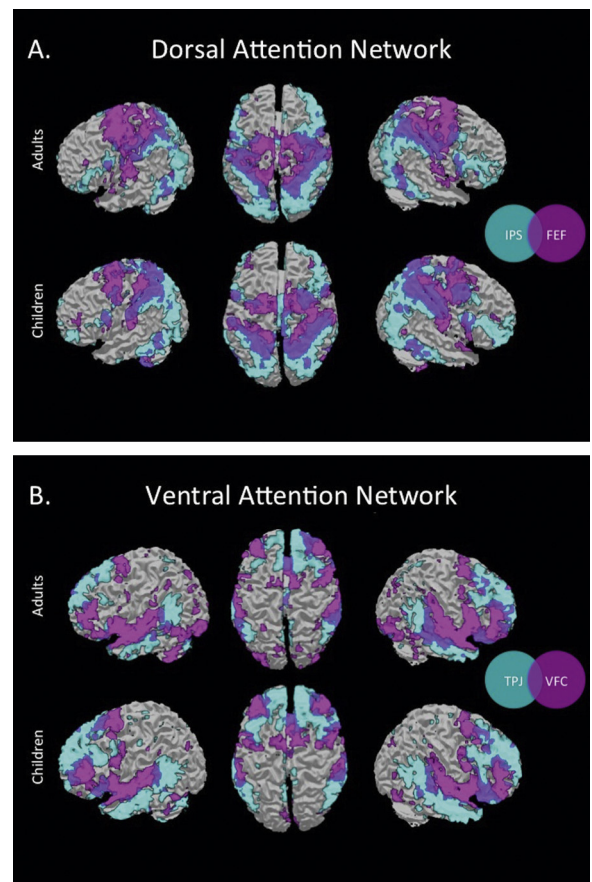


Fig. 1. Conjunction of correlation maps. (A) Voxels significantly correlated with the IPS (blue), FEF (purple), and both, defined as the dorsal attention network (DAN; violet). (B) Voxels significantly correlated with the TPJ (blue), VFC (purple), and both, defined as the ventral attention network (VAN; violet). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

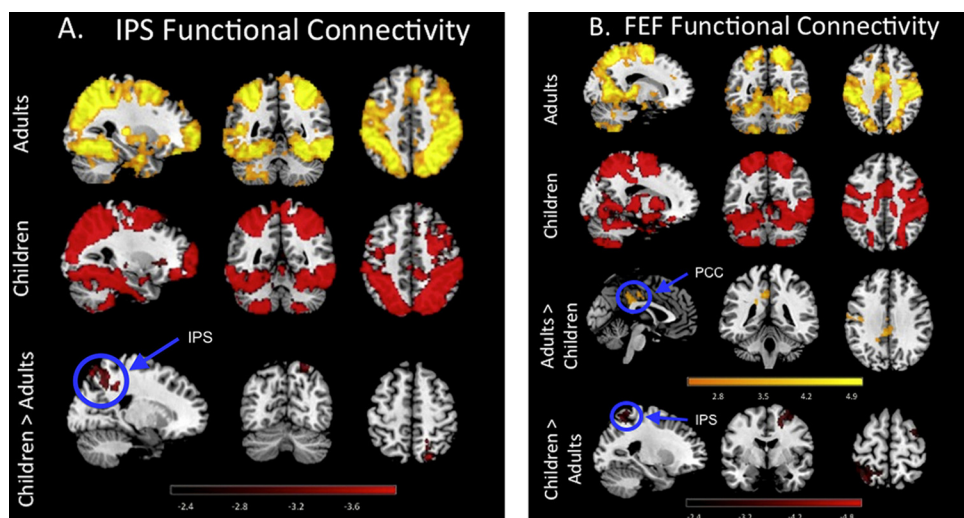


Fig. 2. Individual and group comparisons of resting state functional connectivity of seed ROIs IPS (A) and FEF (B). Yellow maps (first panel) show individual one sample *t*-test for adults. Red maps (second panel) show individual one sample *t*-test for children. Remaining panels show two-sample *t*-tests comparing adults with children. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2

Group differences in functional connectivity of DAN and VAN ROIs.

Seed	Contrast	Functional connectivity	MNI coordinates			Z-score	Cluster size (voxels)
			x	y	z		
FEF	Children > adults	Left superior parietal lobule/superior LOC	−30	−58	58	4.7216	611
	Children > adults	Right precentral gyrus	24	−10	44	5.4054	492
	Adults > children	Left posterior cingulate gyrus	−6	−40	40	3.7597	338
	Adults > children	Left postcentral gyrus	−40	−18	40	3.5311	332
	Adults > children	Left posterior cingulate gyrus	−2	−20	40	3.1041	23
IPS	Children > adults	Right superior LOC	22	−74	58	3.9278	521
TPJ	Adults > children	Left posterior cingulate gyrus	−4	−18	32	4.5237	295
VFC	Children > adults	Left thalamus	0	−24	12	4.8568	1736
	Children > adults	Left insular cortex	−28	24	6	5.1591	814
	Children > adults	Right insular cortex	28	26	6	4.6307	551
	Adults > children	Right temporal pole	34	4	−38	3.7281	332

including VFC and middle frontal gyrus. Strong functional connectivity was also observed between TPJ and regions of the default mode network (posterior cingulate and medial prefrontal cortex). For both adults and children, VFC showed strong functional connectivity with other regions of the VAN including middle frontal gyrus and TPJ (Fox et al., 2006). In addition, strong functional connectivity was observed between VFC and the anterior cingulate cortex (ACC) and insular cortex.

We found that for both ROIs representing the VAN (TPJ and VFC), adults showed greater functional connectivity with regions within the network than children. For the VFC ROI, children showed greater functional connectivity than adults with the anterior insula and ACC, regions comprising the salience network (Seeley et al., 2007) (Fig. 3B).

3.4. Developmental differences in within- and between-network ROI-to-ROI connections

To examine whether between- and within-network functional connectivity patterns show developmental changes, we conducted ROI-to-ROI analyses. No group differences were found for within DAN (IPS-FEF) or within VAN (TPJ-VFC) connections. In other words, children and adults did not differ on strength of functional connectivity within either of the attention networks. Likewise, the between-network ROI comparisons (rIPS-rVFC, rFEF-rTPJ, rIPS-rTPJ, rFEF-rVFC) yielded no significant group differences (Fig. 4).

3.5. Relationship between VAN and salience network

On the basis of our finding that children showed greater functional connectivity of VFC with regions of the

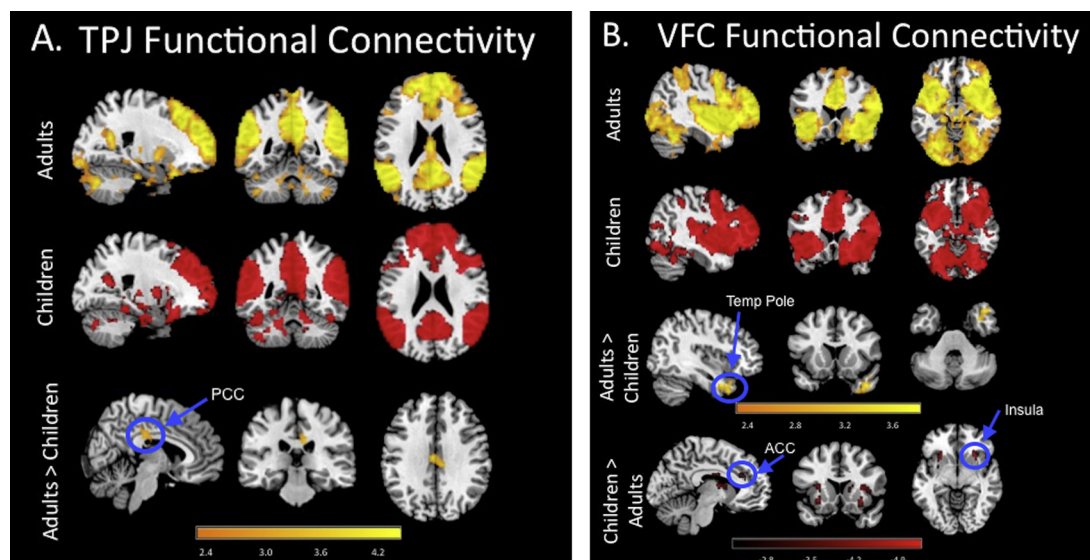


Fig. 3. Individual and group comparisons of resting state functional connectivity of seed ROIs TPJ (A) and VFC (B). Yellow maps (first panel) show individual one sample *t*-test for adults. Red maps (second panel) show individual one sample *t*-test for children. Remaining panels show two-sample *t*-tests comparing adults with children. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

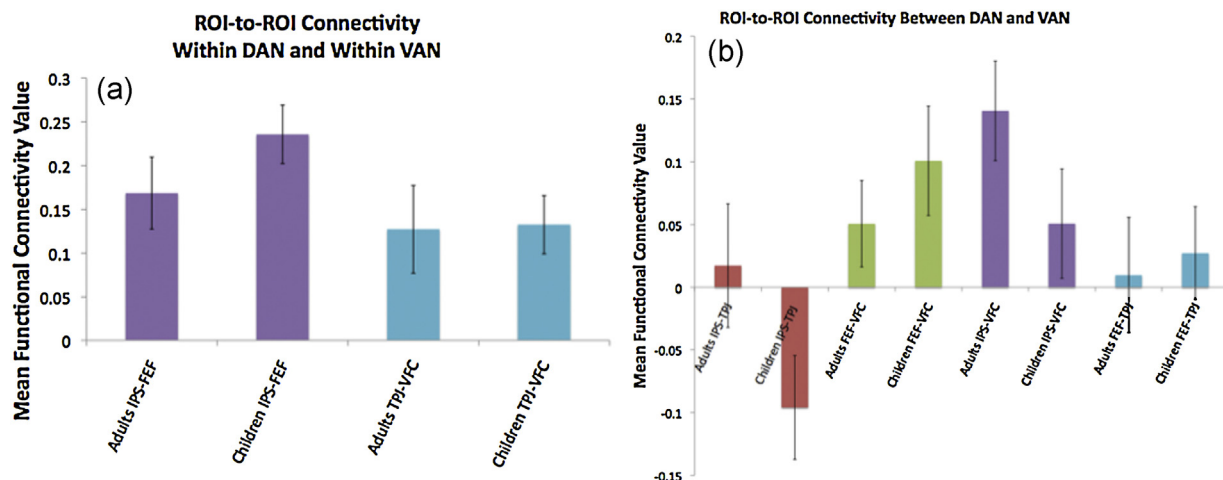


Fig. 4. ROI-to-ROI connectivity within dorsal and ventral attention networks nodes and between dorsal and ventral attention network nodes.

salience network compared with adults, we sought to further explore this finding using ROI-to-ROI comparisons. Upon closer inspection, we noted that the seed from the Fox 2006 paper corresponding to the VFC (42, 20, -6) falls within the anterior insular cortex, a key node of the salience network. To test whether this VFC ROI more accurately reflects a VAN node or a salience network node, we computed functional connectivity of the following: VFC-TPJ (within VAN) and VFC-ACC (within salience network). We reasoned that if VFC-ACC coupling was stronger than VFC-TPJ coupling, then the VFC node might actually be more representative of the salience network than of the VAN. We found that neither VFC-TPJ nor VFC-ACC comparisons showed significant group differences. However, as can be seen in Fig. 5, the VFC ROI showed significantly stronger functional connectivity with ACC (a salience

network node) than with TPJ (a VAN node) in both adults and children ($p < 0.01$). There was a trend suggesting greater connectivity of VFC with ACC in children compared with adults ($p = 0.09$).

4. Discussion

Considerable evidence from behavioral, electrophysiological, and neuroimaging work suggests two anatomically separable fronto-parietal systems for attention exist in the human brain, (1) a dorsal attention network (DAN) involved in top-down orienting, and (2) a ventral attention network (VAN) for bottom-up salience detection (Corbetta and Shulman, 2002). While these neural systems have been well characterized in neuroimaging studies of adults (Corbetta et al., 2008), little is known about the typical development of these brain networks. Here we explored the functional connectivity of the dorsal and ventral attention networks in adults and children using seed-based functional connectivity to explore within- and between-network developmental changes. The current results provide unique insights into the typical development of the DAN and VAN in the human brain. We find asymmetries in functional connectivity patterns associated with key nodes of these attention networks. In both children and adults, the attention networks could be identified as the overlap of functional connectivity maps associated with the IPS and FEF (DAN) and TPJ and VFC (VAN). Thus, children and adults seem to exhibit DAN and VAN network topology that is anchored in these key nodes and is quite similar in overall spatial extent. For the DAN nodes (IPS and FEF), children showed greater functional connectivity with regions within the network compared with adults, whereas adults showed greater functional connectivity between the FEF and extra-network regions including the posterior cingulate cortex. For the VAN, the most striking developmental finding was that children showed greater functional connectivity between VFC and nodes of the salience network (anterior insula and ACC), suggesting

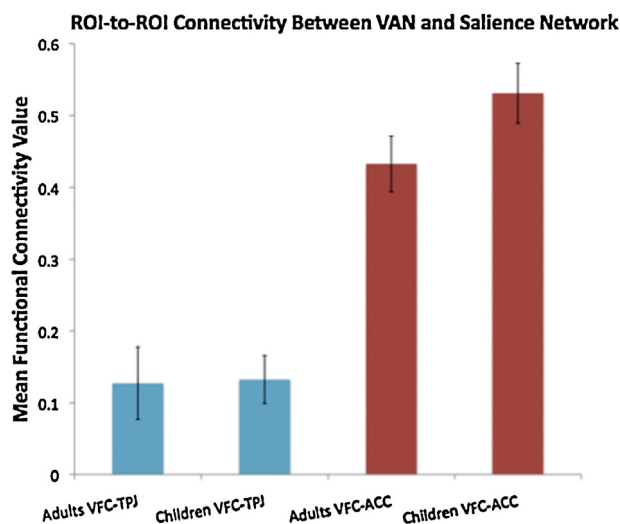


Fig. 5. ROI-to-ROI connectivity between VFC and VAN node (TPJ) and between VFC and salience network node (ACC).

reduced segregation of the VAN and salience networks in childhood compared with adulthood.

4.1. Developmental studies of attention

Evidence from behavioral and neuroimaging studies suggests that specific attention processes undergo protracted periods of developmental maturation. In particular, children are more susceptible to interference and less able to inhibit responses than adults (Bunge et al., 2002). Children show developmental differences such that they exhibit greater activation than adults in anterior cingulate cortex and lateral prefrontal cortices during selective attention (Booth et al., 2003) and response inhibition (Casey et al., 1997). This work is in line with the general developmental principle that brain activation during a particular cognitive task tends to progress from more diffuse to more focal with age (Durstun et al., 2006). Taken together, the findings of decreased task-related frontal activation with age are thought to index the maturation of cognitive strategies from childhood through adolescence and into adulthood (Dumontheil et al., 2010). The development of cognitive control processes has been the focus of the majority of previous investigations (Durstun and Casey, 2006).

Surprisingly little neuroimaging work has examined developmental differences in the relative contributions of the DAN and VAN. A previous study conducted by (Konrad et al., 2005) used a task based fMRI paradigm to explore the development of attention networks for alerting (fronto-parietal), orienting (TPJ and VFC), and executive attention (anterior cingulate/lateral prefrontal) in adults and children. They found that children showed significantly less activation in the right mid-brain regions during alerting, in the right TPJ during reorienting, and in DLPFC during executive control. At the same time, children exhibited significantly more activation in superior frontal gyrus during reorienting and superior temporal gyrus during executive control of attention. The data presented by Konrad et al. (2005) suggest that there is a transition from the immature functional systems that support attentional functions in children to more mature systems in adults.

4.2. Resting state fMRI and brain network development

Over the past ten years, resting state fMRI has emerged as a powerful complementary approach to examination of task-activation. A key principle that has emerged from this literature is that anterior–posterior long-range functional connectivity is slow to develop, particularly in brain networks underlying higher cognitive functions (Fair et al., 2008; Kelly et al., 2009; Supekar et al., 2010). Human brain network development appears to involve simultaneous segregation (decrease of short-range connections) and integration (increase of long-range connections) (Fair et al., 2007). A study using independent component analysis (ICA) found evidence for increased connectivity within the DAN in children compared with adults (Jolles et al., 2011), providing evidence for early segregation of the DAN. In the current study we also find greater within-network connectivity of the DAN in children, particularly in the IPS region, as revealed by group differences in whole-brain

functional connectivity of key DAN nodes. The ROI-to-ROI connectivity (IPS-FEF) corroborated these findings of greater within-DAN connectivity in children, though the effect was not significant.

For the DAN, adults showed greater functional connectivity of the FEF with regions outside the network including the PCC, a key hub of the default mode network (Greicius et al., 2003; Raichle et al., 2001). This increased communication between the DAN and the default mode network observed in adults compared with children might enable greater top-down attentional capacities in adulthood (Rubia, 2013). The ability to modulate or suppress default mode network activity has been linked with successful goal-directed attention and cognition (Anticevic et al., 2012). The same direction of effects was observed for the VAN, where we observed greater functional connectivity of the TPJ with PCC and the VFC with temporal pole in adults compared with children. Overall, it appears that adults exhibited more flexible patterns of extra-network connections of attention network nodes compared with children. These results are largely consistent with previous work demonstrating increasing long-range functional connectivity strength with development (Uddin et al., 2010).

4.3. Ventral attention network and salience network

The VFC in the VAN showed greater functional connectivity in children compared with adults, particularly with ACC and anterior insula. The ROI selected to represent VFC was centered at MNI coordinates 42, 20, –6 based on previous work (Fox et al., 2006). Upon closer examination, this region appears to fall within the anterior insular cortex, and is anatomically very close to a region located at 39, 23, –4 that has been implicated in playing a causal role in switching between the central executive network and the default mode network in adults and children (Uddin et al., 2011). A large body of work indicates that the insula plays a dominant role in detection of novel salient stimuli across multiple modalities (Crottaz-Herbette and Menon, 2006; Downar et al., 2000). The role of the insula in detection of salient stimuli and its inclusion in the “salience network” along with the anterior cingulate cortex has now been well documented (Menon and Uddin, 2010; Seeley et al., 2007). It is worth noting that there is still work to be done to distinguish whether and to what extent the salience network and the so-called “cingulo-opercular network” (Dosenbach et al., 2008) should be conceptualized as distinct entities (Uddin, 2015). To further explore the potential overlap of the VFC node with regions of the salience network, we conducted ROI-to-ROI analyses looking at VFC-TPJ and VFC-ACC connectivity to see which network (the VAN or the salience network) was most closely associated with this ROI. We find that in both adults and children, the VFC shows stronger functional connections to the salience network than to the VAN. We also observed a trend toward greater VFC-ACC connectivity in children compared with adults.

We propose that the VAN and the salience network have overlapping nodes in the region surrounding the VFC and anterior insula. We speculate that in children, these two networks may be less segregated than in adults, and that bottom-up salience processes and attention to

environmental stimuli may be over-represented in the child's brain. Consistent with the "circuit breaker" function attributed to the VAN, it has been demonstrated in adults that signals in the VAN causally influence activity in the DAN (Sridharan et al., 2007). Perhaps the over-connectivity in the VAN in children compared with adults that we observe is a neural signature of the differential and asymmetric maturation of attention processes throughout development. The fact that children exhibit more widespread connectivity in the VFC region may explain why they are behaviorally more susceptible to interruption by environmental stimuli and less able to maintain activities requiring top-down attentional control (Bunge et al., 2002). An alternative speculation is that this VFC region may need to be extensively connected in childhood to ensure detection of salient environmental stimuli, which would be important for basic survival.

Our results are somewhat consistent with the previous task activation study (Konrad et al., 2005). However, we provide evidence to suggest that the second anatomical component of the reorienting network, VFC, shows greater functional connectivity for children than in adults with regions of the salience network. We argue that the reason for this region showing more widespread functional connectivity in children than in adults is because of its anatomical location. We show that the VFC, which is anatomically very close to the anterior insula cortex, is significantly correlated with the ACC. The anterior insular cortex and ACC has been described as the core that forms the salience network, which is important for the facilitation and detection of environmental stimuli (Uddin, 2015). The attention characteristics of the salience network are somewhat similar to those characteristics of the VAN; both are thought to be important for detection of stimuli outside of direct focus. The anatomical proximity of anterior insula and VFC points toward a linkage between the two regions and possibly the shared responsibilities of salience detection. We see that in children, these two salience detection systems are less segregated than in adults. Future work will explore the extent to which segregation between the VAN and salience network throughout development relates to increased attentional abilities using behavioral and task-based neuroimaging paradigms.

4.4. Limitations

The field has not yet come to a consensus as to best practices for dealing with motion artifacts in resting-state fMRI data, though it is clear that such artifacts can bias results (Power et al., 2012; Van Dijk et al., 2012). There have not yet been validation studies to determine the exact effects of the motion scrubbing procedure that has been put forth as a potential solution. We believe that the effects of motion scrubbing on group differences functional connectivity in developmental contexts will require additional methodological study.

A limitation of the current study is that age is dichotomized, rather than continuously examined. We opted to examine the development of attention networks using two age categories in the current study for the following reasons. One was to avoid the period of puberty,

which occurs during adolescence, and is accompanied by protracted (and not very well-characterized) changes in functional connectivity patterns (Blakemore et al., 2010). Given the as yet unknown effects of puberty on development of attention networks in the brain, and the fact that in the current sample participants' pubertal status was not explicitly characterized, we chose to avoid examining the adolescent age range in the current study. We believe that careful consideration of pubertal status is a very important question for future research (Uddin et al., 2013).

The second reason age was dichotomized was due to the sample available in the public dataset that was utilized in the study. As there were not a large enough number of subjects to examine age continuously, we chose to simplify by comparing children and adult groups, as several previous developmental neuroimaging studies have done (Jolles et al., 2011; Kelly et al., 2009; Supekar et al., 2010; Uddin et al., 2011). We believe that an important direction for future research will be to examine this question in larger datasets containing more individuals at various developmental stages in order to examine more complex maturational patterns.

5. Conclusion

The current study demonstrates asymmetric developmental patterns of functional connectivity of the dorsal and ventral attention networks of the human brain. Whereas for the DAN nodes (IPS and FEF), children show greater functional connectivity with regions within the network compared with adults, and adults showed greater functional connectivity between with extra-network regions including nodes of the default mode network, for the VAN nodes (TPJ and VFC), adults showed greater functional connectivity with regions within the network compared with children and children showed greater functional connectivity between VFC and nodes of the salience network. We suggest that because the VFC is within close proximity of anterior insula, an important hub within the salience network, there may be overlap between the VAN and salience network at this node. This asymmetric pattern of development of attention networks may be a neural signature of the shift from over-representation of bottom-up attention mechanisms to greater top-down attentional capacities that emerge between childhood and adulthood. Future research should explore how alterations in development of these attention networks might impact developmental disorders of attention including attention deficit/hyperactivity disorder (ADHD) (Vaidya, 2012).

Conflict of interest

None declared.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.dcn.2015.02.001>.

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